RELATIONSHIPS BETWEEN UNDIGESTED AND PHYSICALLY EFFECTIVE FIBER IN LACTATING DAIRY COWS

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INTRODUCTION

Economic, environmental, and even social considerations are encouraging the use of more forage in dairy cattle rations (Martin et al., 2017). Although regional economics and forage availability may determine the balance between dietary forage and non-forage sources of fiber, we appear to be at the threshold of a new era in our ability to effectively feed fiber to lactating dairy cows. Nutritionists have long realized that neutral detergent fiber (NDF) content alone does not explain all of the observed variation in dry matter intake (DMI) and milk yield as forage source and concentration in the diet vary. Incorporating measures of fiber digestibility and particle size improves our ability to predict feed intake and productive responses.

Waldo et al. (1972) recognized that NDF needed to be fractionated into digestible and indigestible pools for calculation of digestion rates. The recognition that there is an indigestible portion of fiber led to research that improved our understanding of the digestibility of fiber in ruminant diets and the beginning of dynamic models of fiber digestion. Research has focused on a three-pool model of ruminal NDF digestion: indigestible NDF measured as undigested NDF at 240 hours of in vitro fermentation (uNDF240) plus a fast- and slow-fermenting pool of NDF (Mertens, 1977; Raffrenato and Van Amburgh, 2010; Cotanch et al., 2014). To-date more research has focused on defining biologically relevant digestion pools than particle size pools within the rumen, although both digestion and particle size characteristics of a fiber particle are important for explaining ruminal fiber turnover (Mertens, 2011). In a classic paper, Mertens (1997) laid out a comprehensive system for integrating NDF content and particle size, based on the 1.18-mm dry sieved fraction of particles, known as physically effective NDF (peNDF). Although the peNDF system is based solely on particle size as a measure of physical form, it explains a substantial amount of the variation in chewing activity, ruminal pH, and milk fat elicited among forage sources.

Recently, we have focused on the relationship between undigested and physically effective NDF at the Institute, and have conducted a study designed to assess the relationship between dietary uNDF240 and particle size measured as peNDF. The potential interaction between peNDF and uNDF240 is a hot topic among nutritionists with several practical feeding questions being asked in the field:

- What are the separate and combined effects of peNDF and uNDF240 in diets fed to lactating cows?
- Can we adjust for a lack of dietary peNDF by adding more uNDF240 in the diet?

- Similarly, if forage uNDF240 is higher than desired, can we at least partially compensate by chopping the forage finer to maintain feed intake?

The bottom line question becomes: are there optimal peNDF concentrations as uNDF240 content varies in the diet and vice versa? The answer to this question will likely be affected by the source of fiber: forage or non-forage, since they differ dramatically in fiber digestion pools and particle size. Some nutritionists have even questioned how important particle size actually is as we better understand fiber fractions (i.e., fast, slow, and uNDF240) and their rates of digestion. This is a complicated question, but the short answer is – yes – particle size is important, although maybe for reasons we haven't always appreciated, such as its effect on eating behavior even more so than rumination.

MINER INSTITUTE STUDY:
UNDIGESTED AND PHYSICALLY EFFECTIVE FIBER

Dietary Treatments: peNDF and uNDF240

To begin addressing the questions above, we conducted a study in 2018 to assess the effect of feeding lower (8.9% of ration DM) and higher (11.5% of ration DM) uNDF240 in diets with either lower or higher peNDF (19 to 20 versus ~22% of ration DM). The diets contained approximately 35% corn silage, 1.6% chopped wheat straw, and chopped timothy hay with either a lower physical effectiveness factor (pef; fraction of particles retained on ≥1.18-mm screen; 0.24) or a higher pef (0.58).

Table 1. Ingredient and chemical composition of experimental diets (% of DM).

	Low uNDF240[1]		High uNDF240	
	Low peNDF[2]	High peNDF	Low peNDF	High peNDF
Ingredients				
Corn silage	34.7	34.7	34.7	34.7
Wheat straw, chopped	1.6	1.6	1.6	1.6
Timothy hay, short chop	10.5	---	24.2	---
Timothy hay, long chop	---	10.5	---	24.2
Beet pulp, pelleted	12.9	12.9	0.4	0.4
Grain mix	40.3	40.3	39.1	39.1
Composition				
Forage	46.8	46.8	60.5	60.5
aNDFom[3]	33.1	33.3	35.7	36.1
uNDF240om	8.9	8.9	11.5	11.5
peNDFom	20.1	21.8	18.6	21.9
peuNDF240[4]	5.4	5.9	5.9	7.1

[1]Undigested NDF at 240 h of in vitro fermentation.
[2]Physically effective NDF.
[3]Amylase-modified NDF on an organic matter (OM) basis.
[4]Physically effective uNDF240 (physical effectiveness factor x uNDF240).

We used a Haybuster (DuraTech Industries International, Inc., Jamestown, ND) with its hammer mill chopping action to achieve the two particle sizes of dry hay. In addition, for the lower forage diets we partially replaced the timothy hay with nearly 13% pelleted beet pulp to help adjust the fiber fractions. The lower uNDF240 diets contained about 47% forage and the higher uNDF240 diets contained about 60% forage on a DM basis (Table 1).

A New Concept: Physically Effective uNDF240

To explore the relationship between physical effectiveness and uNDF240 among these four diets, we calculated a “physically effective uNDF240” (peuNDF = pef x uNDF240). In Table 1 we see that this value ranged from 5.4% of DM for the lowUNDF240/low peNDF diet to 7.1% of DM for the high uNDF240/high peNDF diet. And by design, the two intermediate diets contained 5.9% of ration DM. A key assumption underpinning our focus on a peuNDF value is that uNDF240 is uniformly distributed across the particle size fractions, particularly above and below the 1.18-mm screen when a sample has been dry sieved. We are currently addressing that question in our Forage Research Laboratory at the Institute.

When feeding these four diets, we expected the bookend diets to elicit predictable responses in DMI based on their substantial differences in uNDF240 and particle size (Harper and McNeill, 2015). We considered them as “bookends” because these diets represent a range in particle size and indigestibility that would reasonably be observed in the field for these types of diets. And most importantly, we wondered if the two intermediate diets would elicit similar responses in DMI given their similar calculated peuNDF content.

In fact, the high uNDF240/high peNDF diet did limit DMI compared with the lower uNDF240 diets (Table 2). When lower uNDF240 diets were fed, the peNDF did not affect DMI. But, a shorter chop length for the higher uNDF240 diet boosted DMI by 2.5 kg/d. As a result, NDF and uNDF240 intakes were highest for cows fed the high uNDF240 diet with smaller particle size. Overall, and as expected, uNDF240 intake was greater for the higher versus lower uNDF240 diets. But, the important take-home result is the 0.45% of BW intake of uNDF240 for cows fed the high uNDF240 diet with hay that had been more finely chopped. The intake of peNDF was driven first by the uNDF240 content of the diet, and then by particle size within each level of uNDF240 (Table 2).

The intake of peuNDF (calculated as the product of pef and uNDF240) was stretched by the bookend diets: 1.47 versus 1.74 kg/d for the low/low versus high/high uNDF240/peNDF diets, respectively. And of greatest interest, we observed that the two intermediate diets resulted in similar peuNDF intake; we were able to elicit the same intake response by the cow whether we fed lower uNDF240 in the diet chopped more coarsely, or whether we fed higher dietary uNDF240, but with a finer particle size.

Table 2. Dry matter and fiber intake for cows fed diets differing in uNDF240 and peNDF.

	Low uNDF240[1]		High uNDF240		SE	*P*-value
Measure	Low peNDF[2]	High peNDF	Low peNDF	High peNDF		
DMI, kg/d	27.5^{a}	27.3^{a}	27.4^{a}	24.9^{b}	0.6	<0.01
DMI, % of BW	4.02^{a}	4.04^{a}	3.99^{a}	3.73^{b}	0.10	0.03
NDF intake, kg/d	9.12^{b}	9.06^{b}	9.74^{a}	8.96^{b}	0.19	0.008
uNDF240om[3] intake, kg/d	2.41^{c}	2.43^{c}	3.11^{a}	2.87^{b}	0.05	<0.001
uNDF240om intake, % of BW	0.35^{c}	0.36^{c}	0.45^{a}	0.43^{b}	0.01	<0.001
peNDFom intake, kg/d	5.56^{b}	5.94^{a}	5.07^{c}	5.44^{b}	0.11	<0.001
peuNDF240[4] intake, kg/d	1.47^{c}	1.59^{b}	1.61^{b}	1.74^{a}	0.03	<0.001

[abc]Means within a row with unlike superscripts differ ($P \leq 0.05$).
[1]Undigested NDF at 240 h of in vitro fermentation.
[2]Physically effective NDF.
[3]Organic matter.
[4]Physically effective uNDF240 (physical effectiveness factor x uNDF240).

Lactational Responses to peNDF and uNDF240

A key question becomes: does lactation performance follow these observed responses in feed intake? Generally, milk and energy-corrected milk (ECM) production responded similarly to peuNDF intake (Table 3). In particular, production of ECM was lowest for cows fed the high/high uNDF240/peNDF diet and greatest for the low/low diet (Table 3). Tracking with DMI, the ECM yield was similar and intermediate for the low/high and high/low uNDF240/peNDF diets. Interestingly, milk fat percentage appeared to be more related to dietary uNDF240 than peNDF content. More research is needed to understand the relative responsiveness of milk fat to uNDF240 and peNDF.

Table 3. Milk yield, composition, and efficiency of solids-corrected milk production.

	Low uNDF240[1]		High uNDF240		SE	*P*-value
Measure	Low peNDF[2]	High peNDF	Low peNDF	High peNDF		
Milk, kg/d	46.1^{a}	44.9^{ab}	44.0^{bc}	42.6^{c}	0.9	<0.01
Milk fat, %	3.68^{b}	3.66^{b}	3.93^{a}	3.92^{a}	0.10	0.03
Milk true protein, %	2.93^{a}	2.88^{ab}	2.96^{a}	2.84^{b}	0.06	0.04
Milk urea N, mg/dl	8.5^{c}	9.4^{bc}	10.1^{ab}	11.0^{a}	0.6	<0.01
Energy-corrected milk, kg/d	47.0^{a}	45.7^{ab}	46.4^{ab}	44.6^{b}	0.9	0.03
ECM/DMI, kg/kg	1.71^{ab}	1.68^{b}	1.70^{ab}	1.79^{a}	0.04	0.02

[abc]Means within a row with unlike superscripts differ ($P \leq 0.05$).
[1]Undigested NDF at 240 h of in vitro fermentation.
[2]Physically effective NDF.

Milk true protein appeared to be boosted by lower peNDF and cows fed the high/high uNDF240/peNDF diet had the lowest milk protein percentage, with cows fed the low/high uNDF240/peNDF diet being intermediate (Table 3). The MUN concentration was reduced first as dietary uNDF240 decreased, and then as peNDF decreased within a level of uNDF240.

Chewing Response to peNDF and uNDF240

Dietary uNDF240 and peNDF had a greater impact on eating than ruminating time (Table 4). This observation that dietary fiber characteristics may have a substantial effect on chewing during eating and time spent eating has been observed in multiple studies. A recent review found that higher forage content, greater NDF or peNDF content, and(or) lower NDF digestibility may all increase time spent eating for a wide range of forages (Grant and Ferraretto, 2018). The cows in our study spent up to 45 min/d more or less eating depending on the diet (Table 4). In fact, cows on the high/high uNDF240/peNDF diet spent 45 min/d longer eating and yet consumed nearly 3 kg/d less DM than cows fed the low/low uNDF240/peNDF diet. An important and practical management question is whether or not cows would have sufficient time to spend at the bunk eating with greater dietary uNDF240 that is too coarsely chopped? And if we consider an overcrowded feedbunk environment, the constraint on feeding time could be even more deleterious.

Cows fed the high/high peNDF/uNDF240 diet had the greatest eating time compared with cows fed the low uNDF240 diets (Table 4). Finely chopping the hay in the high uNDF240 diet reduced eating time by about 20 min/d and brought it more in-line with the lower uNDF240 diets.

Table 4. Chewing behavior as influenced by dietary uNDF240 and peNDF.

	Low uNDF240[1]		High uNDF240		SE	*P*-value
Measure	Low peNDF[2]	High peNDF	Low peNDF	High peNDF		
Eating time, min/d	255[b]	263[b]	279[ab]	300[a]	12	<0.01
Ruminating time, min/d	523	527	532	545	16	0.36

[abc]Means within a row with unlike superscripts differ ($P \leq 0.05$).
[1]Undigested NDF at 240 h of in vitro fermentation.
[2]Physically effective NDF.

Part of the reason why eating time was more affected than rumination time is related to the observation that cows tend to chew a bolus of feed to a relatively uniform particle size prior to swallowing. Grant and Ferraretto (2018) summarized research that showed that particle length over a wide range of feeds was reduced during ingestive chewing to approximately 10 to 11 mm (Schadt et al., 2012). Similarly, in our current study, we confirmed that cows consuming all four diets swallowed boli of total mixed ration with a mean particle size of approximately 7 to 8 mm (Table 5) regardless of uNDF240 or peNDF content of the diet.

Table 5. Particle size of swallowed total mixed ration bolus versus diet offered (% retained on sieve; DM basis).

	Sieve size, mm						Mean particle size, mm
Diet	19.0	13.2	9.50	6.70	4.75	3.35	
Low peNDF[1], low uNDF240[2]	3	27	33	20	10	7	9.36
High peNDF, low uNDF240	12	27	29	16	9	6	10.42
Low peNDF, high uNDF240	9	21	23	22	14	11	9.19
High peNDF, low uNDF240	32	13	17	20	11	7	11.55
Bolus							
Low peNDF, low uNDF240	1	11	38	26	14	10	7.96
High peNDF, low uNDF240	3	11	22	29	20	16	7.46
Low peNDF, high uNDF240	2	11	26	29	19	13	7.51
High peNDF, low uNDF240	5	12	19	28	21	14	7.78

[1]Physically effective NDF.
[2]Undigested NDF at 240 h of in vitro fermentation.

Ruminal Fermentation: peNDF and uNDF240

Mean ruminal pH followed the same pattern of response as DMI and ECM yield (Table 6). Although not significant, time and area below pH 5.8 numerically appeared to be more related with dietary uNDF240 content than peNDF. Total VFA concentration followed the same pattern as DMI, ECM yield, and mean ruminal pH with cows that consumed similar peuNDF240 having similar total ruminal VFA concentrations (Table 6). Tracking with milk fat percentage, the ruminal acetate + butyrate:propionate ratio was more influenced by uNDF240 than peNDF in our study.

When we assessed ruminal pool size and turnover, we found that the pool size of NDF tended to be greater for cows fed higher uNDF240 diets, and that the pool size of uNDF240 was greater for cows fed these same diets (Table 6). Ruminal turnover rate of NDF tended to be slower for cows fed the higher uNDF240 diets with the high/high uNDF240/peNDF diet having the slowest ruminal turnover of fiber. Overall, the differences among diets in ruminal pool size and turnover were small, but it appeared that higher uNDF240 diets increased the amount of uNDF240 in the rumen and slowed the turnover of NDF. The higher ruminal NDF turnover for cows fed the finely chopped high uNDF240 diet helps to explain the observed increase in DMI.

If future research confirms the results of this initial study, it suggests that when forage fiber digestibility is lower than desired, then a finer forage chop length will boost feed intake and lactational response. The enhanced lactational performance was associated with less eating time as well as more desirable ruminal fermentation and fiber turnover for cows fed the higher uNDF240 diet with lower peNDF.

Table 6. Ruminal fermentation and dynamics of fiber turnover.

Measure	Low uNDF240[1] Low peNDF[2]	Low uNDF240 High peNDF	High uNDF240 Low peNDF	High uNDF240 High peNDF	SE	*P*-value
24-h mean pH	6.11[b]	6.17[ab]	6.22[ab]	6.24[a]	0.05	0.03
Time pH < 5.8, min/d	253	208	166	164	61	0.24
AUC, pH < 5.8[3]	52.0	49.6	33.5	30.0	15.0	0.29
Total VFA, m*M*	122.8[a]	120.6[ab]	118.3[ab]	112.3[b]	4.1	0.05
Acetate+butyrate:propionate	3.33[c]	3.39[bc]	3.58[a]	3.54[ab]	0.16	<0.01
Ruminal pool size, kg						
OM	12.7	12.3	12.9	12.4	0.5	0.44
aNDFom	8.2	7.9	8.7	8.4	0.4	0.06
uNDF240om	3.8[b]	3.7[b]	4.5[a]	4.4[a]	0.2	<0.01
Ruminal turnover rate, %/h						
OM	8.7	8.8	8.4	8.0	0.4	0.15
aNDFom	4.4[x]	4.4[x]	4.2[xy]	3.9[y]	0.2	0.04
uNDF240om	2.7	2.8	3.0	2.7	0.1	0.29

[abc]Means within a row with unlike superscripts differ ($P \leq 0.05$).
[xy]Means within a row with unlike superscripts differ ($P \leq 0.10$).
[1]Undigested NDF at 240 h of in vitro fermentation.
[2]Physically effective NDF.
[3]Area under curve pH < 5.8; ruminal pH units below 5.8 by hour.

PRELIMINARY SYNTHESIS: PHYSICALLY EFFECTIVE, UNDIGESTED NDF AND COW RESPONSES

We have combined data from three experiments conducted at the Institute to further explore the relationship between dietary uNDF240 and DMI and ECM yield as well as the relationship between dietary peuNDF240 and DMI and ECM yield. The dietary formulations for these three studies were:

- Study 1: the study just described (see Table 1; Smith et al. 2018a; 2018b).
- Study 2: approximately 50 or 65% forage in the ration DM, with 13% haycrop silage (mixed mostly grass), and between 36 and 55% corn silage (either brown midrib 3 or conventional) in ration DM (Cotanch et al., 2014).
- Study 3: approximately 42 to 60% corn silage (brown midrib 3 or conventional) and 2 to 7% wheat straw (finely or coarsely chopped) in ration DM (Miller et al., 2017).

Details of ration formulation may be found in the references for each study. Importantly, all of the diets fed in these three experiments were based heavily on corn silage, contained some combination of haycrop silage and chopped straw, and in Study 1 (the current study) two of the diets also contained substantial pelleted beet pulp to formulate the lower uNDF240, lower forage diet.

Figures 1 and 2 illustrate the relationships that we observed when we combined the data from these three studies. For these types of diets, both uNDF240 and especially peuNDF240 appear to be usefully related with DMI and ECM production.

At the moment, it is important to restrict these inferences to similar diets (corn silage with hay and fibrous byproducts) because more research is required with varying forage types and sources of uNDF (forage versus non-forage) to determine the robustness of the relationships shown in Figures 1 and 2. In particular, legumes such as alfalfa contain more lignin and uNDF240, but have faster NDF digestion rates than grasses, and we might expect different relationships between dietary uNDF240 and DMI for legume- versus grass-based rations. In fact, research has shown that very high levels of uNDF240 intake may be achieved when lactating cows are fed finely chopped alfalfa hay (Fustini et al., 2017) in part because alfalfa contains more uNDF240 than grasses (Palmonari et al., 2014; Cotanch et al., 2014).

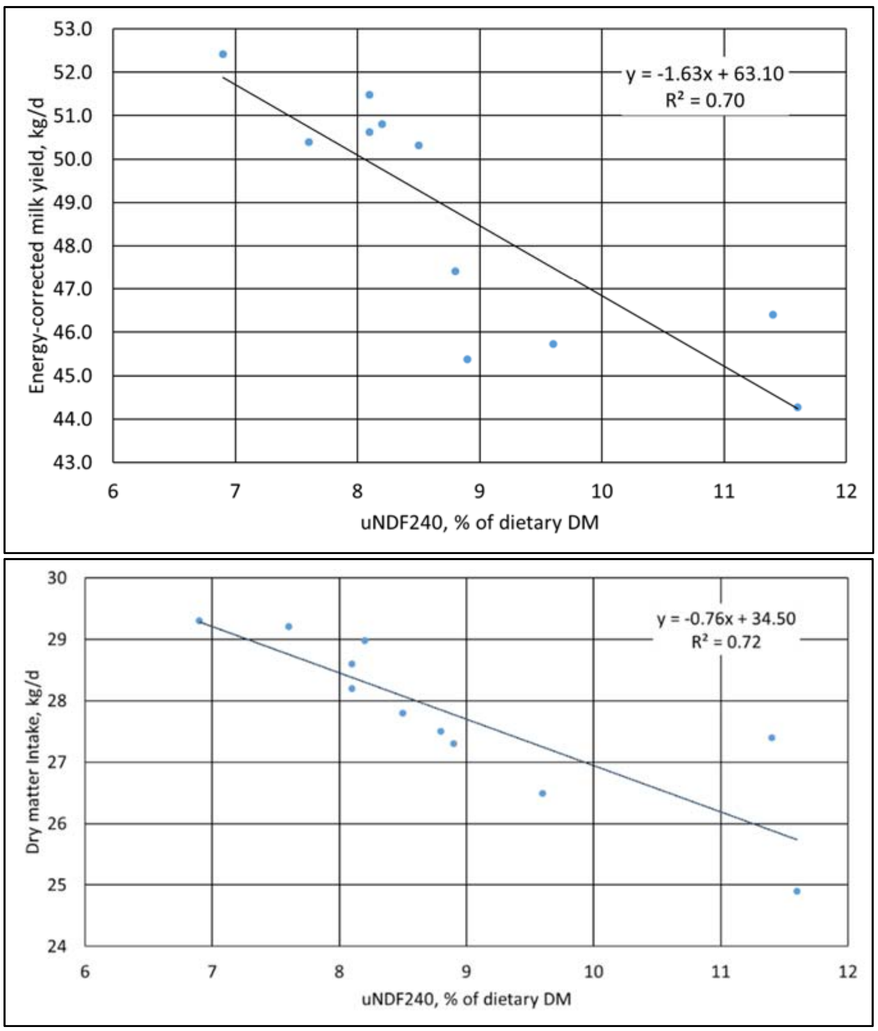

Figure 1. Relationship from three studies between dietary uNDF240 and DMI and ECM yield for cows fed diets based on corn silage, haycrop silage, and chopped wheat straw.

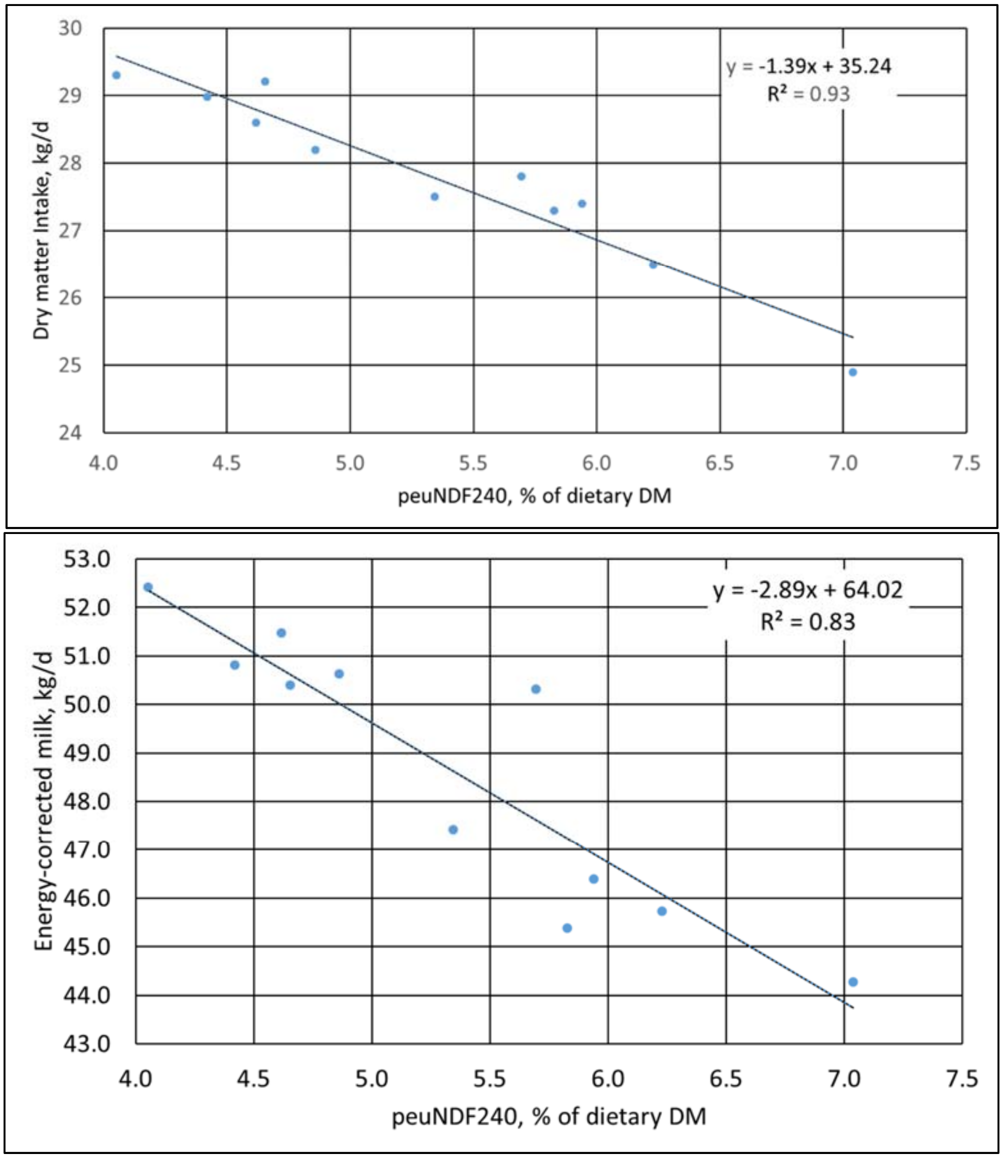

Figure 2. Relationship from three studies between dietary peuNDF240 and DMI and ECM yield for cows fed diets based on corn silage, haycrop silage, and chopped wheat straw (peuNDF240 = physically effective undigested NDF measured at 240 h of in vitro fermentation).

SUMMARY AND PERSPECTIVES: A TALE OF TWO FIBERS

The calculated "physically effective uNDF240" (pef x uNDF240) appears to be a useful concept when interpreting cow response to the diets fed in this study and studies with similar types of diets. Our goal is not to coin yet another nutritional acronym, but to focus on a potentially useful concept. We were able to elicit the same response by the cow whether we fed lower uNDF240 in the diet with greater peNDF, or whether we fed higher uNDF240, but chopped the dry hay more finely. In other words, the peuNDF240, or integration of pef and uNDF240, was highly related to DMI and ECM yield.

If future research confirms this relationship between dietary uNDF240 and DMI, it suggests that when forage fiber digestibility is lower than desired, then a finer forage chop length will boost feed intake and lactational response. In addition to investigating potential and probable differences between legumes and grasses, we also must understand the potential responses to forage and non-forage sources of fiber.

As Charles Dickens wrote in his classic novel *Tale of Two Cities* “It was the best of times, it was the worst of times.” When it comes to fiber, it looks like we can have the best of times when we are able to integrate two measures of fiber – uNDF240 and peNDF - when formulating rations (Grant, 2018). Research is needed to test this relationship in alfalfa-based diets, pasture systems, and other feeding scenarios that differ markedly from a typical Northeastern and upper Midwestern US diet based primarily on corn silage.

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